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Direct and indirect effects of egg parasitism by *Neopolycystus* Girault sp. (Hymenoptera: Pteromalidae) on *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae)

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Running title: Egg parasitism by *Neopolycystus*

Abstract

Neopolycystus sp. is the only primary egg parasitoid associated with the pest beetle *Paropsis atomaria* in subtropical eucalypt plantations, but its impact on its host populations is unknown. The simplified ecosystem represented by the plantation habitat, lack of interspecific competition for host and parasitoid, and the multivoltinism of the host population make this an ideal system for quantifying the direct and indirect effects of egg parasitism, and hence, effects on host population dynamics. Within-, between-, and overall egg batch parasitism rates were determined at three field sites over two field seasons, and up to seven host generations. The effect of exposure time (egg batch age), host density, and proximity to native forest and water sources on egg parasitism rates were also tested. *Neopolycystus* sp. exerts a significant influence on *P. atomaria* populations in *E. cloeziana* plantations in south-east Queensland, causing the direct (13%) and indirect (15%) mortality of almost one-third of all eggs in the field. Across seasons and generations, 45% of egg batches were parasitised, with a within-batch parasitism rate of around 30%. Between-batch parasitism increased up to 5-6 days after oviposition in the field, although within-batch parasitism rates generally did not. However, there were few apparent patterns to egg parasitism, with rates often varying significantly between sites and seasons.

Key words: paropsine, parasitoid, eucalypt

INTRODUCTION

Host-parasitoid interactions are an important ecological component in population dynamics, especially in host population suppression and stability. In natural systems, parasitism may even be considered a powerful contributor to complex, multi-species stability; its ecological role in agricultural ecosystems, however, is less straightforward because changes in patterns of host abundance and distribution accompany the shift to crop habitat (Hassell & Waage 1984). Eucalypt plantations, especially of species planted within their native range, possess a combination of natural and agricultural ecosystem traits that may influence herbivore-parasitoid dynamics within them. For example, large-scale monocultures of even-aged stands support less parasitoid biodiversity than native systems (see Braganca *et al.* 1998; Steinbauer *et al.* 2006). However, plantations can compare favourably to agricultural systems in terms of representing functioning natural communities (see Hartley 2002), and at least where planted

within their native range, are readily colonised both by endemic herbivores and their natural enemies (see Strauss 2001).

Eucalypt plantations are a recent but rapidly expanding landscape feature in the Australian subtropics, with around 90 000 ha established (Parsons *et al.* 2006), and a parallel emergence of pest species is associated with them (e.g. Wylie & Peters 1993; Nahrung 2006). This system is therefore ideal for studying host-parasitoid interactions in a modified natural ecosystem. *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae) is by far the most abundant pest species in *Eucalyptus cloeziana* (F. Muell.) plantations (Nahrung 2006), while *Neopolycystus* Girault sp. (Hymenoptera: Pteromalidae) is its only recorded primary egg parasitoid in south-east Queensland (SEQ) (Nahrung *et al.* unpubl.). Such straightforward two-species interactions are not common in nature (Hassell & Waage 1984), and thus enable the examination of host-parasitoid dynamics in the absence of interspecific competition at both trophic levels. In addition to ecological insight into more complex multi-species interactions, understanding the influence of host-parasitoid interactions on population dynamics in pest populations can be important for pest management, especially integrated pest management and both classical and conservation biological control programs.

Here, we investigate patterns of host use by *Neopolycystus* sp. to estimate its direct and indirect impacts on *P. atomaria* at three field sites over two consecutive seasons with up to seven host generations. Specifically, our intention was to determine temporal, generational and spatial patterns of parasitism using within- and between- batch parasitism rates, as well as the overall effects of parasitism on host populations. We also assessed parasitism in relation to host density and spatial landscape features. This study formed part of a broad series of ecological studies on *P. atomaria* in SEQ hardwood plantations, where its pest status has been recently recognised.

MATERIALS AND METHODS

The study system

Paropsis atomaria has up to four generations per year in SEQ (Nahrung 2006), laying eggs during spring and summer in batches (mean ± se 76 ± 1, range 14-147, M. P. Duffy unpubl.) deposited upright on young shoots, or sometimes leaf tips, forming a ringed cluster with each of the eggs projecting radially (Cumpston 1939). Larvae hatch after 10 - 14 days (Carne 1966) and feed on young, expanding eucalypt foliage. The duration of the larval stage is 3 - 4 weeks

which includes four instars. Like several other paropsine species (see Simmul & de Little 1999), larvae of *P. atomaria* are highly gregarious, particularly in earlier instars (Carne 1966). Larvae defend themselves by elevating their posterior end and everting defensive glands that secrete hydrogen cyanide, benzaldehyde and glucose (Moore 1967). Towards the end of the fourth instar the larvae drop to the ground and form pupal cells several centimetres below the surface (Cumpston 1939). Pupation occurs five days after cell formation and adults emerge approximately ten days later. Females are ready to oviposit three weeks after emergence (Carne 1966).

Neopolycystus sp. was the only primary egg parasitoid reared from *P. atomaria* egg batches in SEQ, although there are other primary parasitoid species associated with *P. atomaria* eggs in temperate regions (Nahrung *et al.* in press; Duffy 2007). To date there are no published data on this undescribed parasitoid species.

General sampling method

Three SEQ *Eucalyptus cloeziana* plantations were sampled for *Paropsis atomaria* eggs parasitised by *Neopolycystus* sp. All sites were planted on past grazing land with trees spaced at 5 x 2 metre intervals. Site details are as follows:

Site I (via Gympie) 26°04′40.72″S 152°44′8.88″E approx. 38 ha planted in May 2002. Altitude range 83.8 - 249 m. Total rainfall during the sample period (October 2004 – April 2005) was 686.5 mm. Mean average daily temperature was 22.48± 0.19°C, maximum mean 28.75°C and minimum mean 13.75°C;

Site II (via Glastonbury) 26°11′20.4″S 152°29′40.2″E approx. 22 ha planted in March 2002. Altitude range 67.7 - 162 m. Total rainfall during the sample period (October 2004 – May 2005) was 620 mm. Mean average daily temperature was 22.66±0.20°C, maximum mean 29.5°C and minimum mean 13.75°C;

Site III (via Gympie) 26°05′97.2″S 152°43′7.54″E approx. 17 ha planted in March 2004. Altitude range 65.8 - 183 m. Rainfall during the 2005/2006 season (October to April) was 677.1 mm. Mean average daily temperature was 23.00±0.19°C, maximum mean 29.75°C and minimum mean 14.25°C.

Sites I and II were monitored during the 2004/2005 season (September to April) and Sites I and III during the 2005/2006 season (October to April) every two weeks. Eight different plots, each comprising a 2-row x 3-tree block, within each plantation were sampled on each census date. In the 2004/2005 season, all egg batches observed were collected, while in the 2005/2006 season, a maximum of five egg batches per plot (*i.e.* up to 40 per plantation)

was collected on each sample date. Although all egg batches observed were collected in the first season, we did not consider that this destructive sampling method would influence subsequent results: each sample was from less than 1% of trees in each plantation, and different trees were sampled on each date. Egg batches remained intact on a 2 – 3 cm length of host stem, and each was collected into a separate plastic vial and transported to the laboratory in a cooled box. In the laboratory, the exact number of eggs per batch was counted, or the number of eggs per batch was estimated using the following equations: 2004/2005 season, $y = 0.556x + 45.071$ where y = number of eggs in batch and x = sum of parasitoids and larvae emerging from batch; 2005/2006 season, $y = 1.107x + 0.1643$ where y = number of eggs in batch and x = length of egg batch multiplied by the number of eggs around base of egg collar (see Duffy 2007 for details). Estimation of egg batch number was used to supplement real count data to reduce processing time in the laboratory. Each egg batch was maintained separately in a cotton-wool capped vial in a controlled temperature cabinet at 24 °C. Egg batches were checked every 1 - 2 days, until larval or wasp emergence, the date of which was recorded, and the number of wasps and larvae that emerged from each batch was counted.

Parasitism rate and exposure time in the field

To ascertain the relationship between exposure time (age of egg batch) and parasitism rate, and to ensure our samples weren't biased by collection frequency of different-aged egg batches (*sensu* Mo & Farrow 1993), we examined parasitism rate as a function of egg batch age. The length of time that eggs were exposed to parasitoids in the field was estimated using lower temperature thresholds (Ltt) and day-degree (DD) development rates calculated from Carne (1966) and spatially interpolated climatic data for each site from the silo data drill (http://www.nrme.qld.gov.au/silo). The number of DD between egg collection and eclosion was determined using the equation

$$LabDD = (24\ °C - 5.6\ °C) * \text{days to hatch in lab}$$

where 24 °C is the constant temperature at which egg batches were housed in the laboratory, and 5.6 °C is the Ltt for egg development (derived from Carne 1966).

The number of DD required in the field was estimated by $(178.6 - LabDD)$, where 178.6 is the number of DD above the Ltt that eggs require to develop. Field DD per day were estimated using mean daily field temperature minus Ltt (5.6 °C), and these were summed backward from each collection date until the required number of DD was reached. The number of calendar days to obtain the required DD in the field was then determined. Five egg

batch field exposure times were used in analyses: 0-2 days, 3-4 days, 5-6 days, 7-8 days and 9-10 days. Between- and within-batch parasitism rates were compared between these age-classes for the whole season. Proportions were arcsine-square root transformed prior to ANOVA, and post-hoc comparisons were made using Fisher's LSD test.

Direct effects of egg parasitism: between- and within-batch parasitism rates across host generations, sites and seasons

Between-batch parasitism rates (number of egg batches with parasitoids emerging/total number of egg batches collected) were determined for each sample date at each site, and for each host generation. Host generations were defined during population censes for a separate study (Duffy 2007). Within-batch parasitism rates (number of parasitoids emerged/number of eggs per parasitised batch) were also calculated for each sample date at each site, and for each generation. Total effective parasitism rates (total number of parasitoids emerged/total number of all eggs) were calculated to provide a measure of the impact of *Neopolycystus* sp. on its host population overall. All hyperparasitoids were obligate (Tribe 2000, Duffy 2007) and therefore required primary parasitisation by *Neopolycystus* sp., so emergent hyperparasitoids were included in calculations as *Neopolycystus* sp., while batches from which neither parasitoids nor host larvae emerged were excluded from all analyses. A Bonferroni adjustment was applied where each data set was used for multiple comparisons ($P = 0.004$).

Indirect effects of egg parasitism

The proportion of unhatched eggs per batch (those that failed to produce either a wasp or a host larva) was compared between parasitised and unparasitised batches to determine whether the presence of egg parasitoids influenced egg mortality. Proportions were arcsine-square root transformed and compared using t-tests. Total mortality rates (parasitised eggs + unhatched eggs) were compared with the stage-specific mortality rates reported by Duffy (2007) to estimate the overall impact of egg parasitoids on egg mortality.

Egg parasitism may also indirectly impact on host mortality if smaller larval cohort sizes are less able to initiate feeding than larger groups (*sensu* Nahrung *et al*. 2001). We tested this hypothesis in the laboratory with *P. atomaria*. Different egg parasitism rates (95, 90, 80, 60, 45, 30 and 15 percent) were simulated by placing eleven replicates of the five smaller larval groups (4, 8, 15, 30 and 42 larvae) and 6 replicates of the larger groups (53, 65 and 76

larvae) onto freshly expanded, new season *E. cloeziana* foliage in the laboratory. Initial densities were established using unfed (except for egg chorion consumption - see Carne 1966) neonate larvae which were transferred to the *E. cloeziana* foliage using a fine paint brush. Replicates were held in a constant temperature cabinet (24°C; 16L:8D photoperiod) for one week, with mortality for the preceding twenty-four hours recorded daily when new foliage was added. Proportions were arcsine-square root transformed and analysed using ANOVA.

Parasitism rates and host density

Between-batch parasitism rates were examined for relationships with host density using Pearson correlation for the proportion of egg batches parasitised per sample date against the number of egg batches collected per sample. Within-batch parasitism rates were likewise examined against host density to test whether when fewer batches are available more eggs per batch are parasitised.

Additionally, the proportion of parasitised egg batches per plot for each sample date was determined for Site I and Site II 2004/2005 and used to relate host density to parasitism rates. Only sections from which five or more egg batches were collected were considered in analyses. Linear regression (number of egg batches collected against the proportion of egg batches parasitised) was used to determine whether there was a statistical relationship between these parameters. Our hypothesis was that a significant relationship between host density and parasitism rates may indicate that wasps are better able to locate or utilise large patches of egg batches compared with small patches.

Parasitism rate in relation to plantation landscape features

To test the idea that key requirements of natural enemies such as the availability of alternative foods (Gurr & Nicol 2000; Berndt *et al.* 2002; Rebek *et al*. 2005), shelter or refugia (Wratten & van Emden 1995; Langellotto & Denno 2004) and alternative prey or hosts (van Emden 1990) can affect parasitoid populations, egg batch parasitism rates were related to distance from native eucalypt forest and nearest water source. These landscape features have the potential to provide a number of the key requirements listed above. The latitude and longitude of each sample plot (described in sampling methods) and landscape feature was recorded using Global Positioning System (GPS) and plotted using Garmin Mapsource version 6.3. Distances from each sample point to the nearest native eucalypt forest and water source were

then measured using Mapsource. Correlations between distance from landscape features and proportion of egg batches parasitised were then carried out for Sites I and II in 2004/2005 and Sites I and III in 2005/2006.

RESULTS

Parasitism rates and exposure time in the field

The number of egg batches parasitised increased up to 5-6 days after being laid, but few or no additional egg batches were parasitised after this time in the field at all sites (Figure 1). In contrast, within-batch parasitism rates did not significantly increase depending on exposure time, except at Site II during the 2004/2005 season (Figure 2) (ANOVA, Site I 04/05: $F_{4,237}$= 1.6, P = 0.17; Site II 04/05: $F_{4,160}$= 8.5, P < 0.001; Site I 05/06: $F_{4,75}$= 0.52, P = 0.72; Site III 05/06: $F_{4,76}$= 2.14, P = 0.09). Collection frequency of egg batches collected before and after the critical 5-6 day period was similar: 55% of batches were collected prior to maximum parasitisation, and 45% after; we therefore did not need to adjust general collection data for field exposure time.

Direct effects of egg parasitism: between- and within-batch parasitism rates across host generations, sites and seasons

On average, around 45 % of egg batches were parasitised at our study sites between 2004 and 2006. The overall proportion of egg batches parasitised was lowest at Site III (around 30 %) (Table 1), while about half of all egg batches were parasitised at Site I (both seasons) and Site II. Overall mean within-batch parasitism rates varied by a maximum of 9 % (22-31 %) and this difference was significant only between Sites I and II in the 04/05 season (Table 1). Within-batch parasitism rates varied significantly throughout the season at both sites during the 04/05 season, but at neither site during 05/06. Within- and between- batch parasitism rates did not vary significantly between host generations throughout the season (Figure 2). There were no trans-seasonal patterns in between-batch parasitism rates for any site/season combinations (Pearson correlations = 0.70, 0.51, -0.54, P > 0.02) (Figure 2). The effective parasitism rate (the impact of egg parasitoids on the population as a whole *i.e.* total number of parasitoids over total number of eggs) averaged 13% for all sites and seasons, and did not differ significantly at Site I between seasons (Table 1).

Indirect effects of egg parasitism

The proportion of unhatched (into wasps or larvae) eggs was significantly higher from batches that were parasitised than for unparasitised batches at all sites in both seasons (Figure 3) (t-tests: Site I 04/05 t_{395}=9.3 P< 0.001; Site II 04/05 t_{241}=5.5 P< 0.001; Site I 05/06 t_{170}=4.3 P< 0.001; Site III 05/06 t_{243}=2.9 P= 0.004). On average, parasitism doubled egg failure, resulting in an additional 14.8 ± 3 % egg mortality to unparasitised eggs (normally 15 ± 3 %).

Overall *P. atomaria* egg-early instar field mortality is about 70 % (Duffy 2007). About 15% of egg mortality can be attributed to average failure of eggs to hatch (see above). The estimated overall direct loss from egg parasitoids was 13 % (Table 1), with an additional 15 % lost as an indirect effect of parasitism (Figure 3). Thus, egg parasitoids contribute directly and indirectly to almost half of the estimated egg mortality in the field, and are responsible for mortality of about one-third of all eggs in the field. The remaining egg-early instar field mortality probably arises from predation of egg batches and failure of early instars to initiate feeding on host foliage. For example, predation of *P.atomaria* eggs by *Oechalia schellenbergii* Guérin-Méneville (Hemiptera: Pentatomidae) has been frequently observed in *E. cloeziana* plantations in south-east Queensland (Lawson pers. obs.).

Egg parasitism is unlikely to contribute indirectly to host mortality further by the establishment of larval feeding establishment through reduced larval batch size, as overall there was no significant effect of initial batch size on neonate larval survival of *P. atomaria* ($F_{7,70}$ = 1.962, P = 0.074). The only exception was the smallest batch size, where the mortality rate was approximately double that of any other batch (Figure 4).

Parasitism rate and host density

There was a significant, positive correlation between the proportion of eggs parasitised and the number of egg batches present on branches at Site I in the 2004/2005 season (Pearson correlation = 0.62, P = 0.02). At Site II in the same season, there was no significant relationship between parasitism rate and the number of egg batches censused (Pearson correlation = 0.21, P = 0.51). Site III, in contrast, showed a significant, negative correlation between these parameters (Pearson correlation = -0.74, P = 0.01).

This pattern of inconsistency was repeated when comparing host density and parasitism: host density (number of egg batches collected) was significantly correlated with the proportion of egg batches parasitised at Site I (linear regression: $y = 0.027x + 0.1701$, R^2=

0.48, P < 0.001) but not at Site II (linear regression: $y = 0.0033x + 0.5153$, $R^2 = 0.008$, P = 0.68). Because a maximum of five egg batches was collected per plantation section in the 2005/2006 season, these data were not tested in this way.

The proportion of eggs parasitised within batches (*i.e.* within-batch parasitism rates) increased with increases in the proportion of batches parasitised (*i.e.* between-batch parasitism rates) at Site I (04/05) and at Site III (05/06) (Pearson correlations: 0.59, P = 0.03; 0.74, P = 0.01, respectively), but there was no such relationship at Site II (04/05) or Site I (05/06) (Pearson correlations: 0.28, P = 0.47; -.22, P = 0.52). Within-batch egg parasitism rates were not related to host density at any site.

Parasitism rate in relation to plantation landscape features

In general there was no correlation between distance from nearest native eucalypt forest or water and the proportion of *P. atomaria* egg batches parasitised or within batch parasitism rate at any of the three plantations (Table 2). The only exceptions were a weak negative correlation between distance from forest and within batch parasitism rate at Site III (05/06), and a weak positive correlation between distance from water and proportion of egg batches parasitised at Site I (04/05).

DISCUSSION

Neopolycystus sp. exerts a significant influence on *P. atomaria* populations in *E. cloeziana* plantations in south-east Queensland, causing the direct and indirect mortality of almost one-third of all eggs in the field. Across seasons and generations, 45% of egg batches were parasitised, with a within-batch parasitism rate of around 30%. Additionally, parasitised batches exhibited twice the egg failure rate of unparasitised batches: probably the result of parasitoids failing to develop, possibly through superparasitism. Tribe (2000) and Nahrung and Murphy (2002) likewise recorded high levels of unviable paropsine eggs following exposure to egg parasitoids.

We demonstrated no further indirect effects of egg parasitism, although in other paropsine species smaller larval groups (e.g. those with higher within-batch egg parasitism rates) are less able to initiate feeding than larger groups (Nahrung *et al*. 2001). Thus we hypothesised that higher egg parasitism rates may indirectly increase mortality by reducing the group size of remaining larvae. Our hypothesis was not supported, with a difference in

larval mortality recorded only in the smallest larval group tested (equivalent to ~95% parasitism). The reason proposed for larger groups being more able to establish feeding is that the probability of one larva successfully initiating feeding, thereby creating access to a suitable feeding site, increases as group size increases (Nahrung *et al.* 2001). *Paropsis atomaria* egg batches are much larger than those of the species studied by Nahrung *et al.* (2001), so any more than 5% larval emergence from an egg batch probably provides sufficient individuals to ensure feeding establishment.

At all sites and seasons, between-batch parasitism rates generally increased with field exposure time up to 5-6 days after oviposition; presumably after this time eggs became behaviourally unrecognisable or physiologically unsuitable to *Neopolycystus* sp. Tribe (2000) reported that for *Trachymela tincticollis* (Chrysomelidae: Paropsini) eggs, the window for successful egg parasitisation was around 3 days in the laboratory. In contrast, within-batch parasitism rates did not show a parallel increase with exposure time, suggesting that once a batch has been parasitised it too becomes unsuitable/unrecognisable as a host, despite availability of unparasitised eggs within it (although all eggs within a batch can be parasitised in the field – see Results). However, in half of the sites/seasons examined here, within-batch parasitism rates increased as between-batch parasitism rates increased. There was no consistent relationship between within- or between-batch parasitism rates and host density. Density-dependent aggregation by parasitoids in patches of high host density may not be as important as once thought (Hassell 2000), but more research into host-location mechanisms used by *Neopolycystus* sp. is required to provide a greater understanding of this host-parasitoid system.

There were no clear trends for proximity to native forest or water sources and parasitism rates, although the characteristics of the surrounding habitat can influence parasitism rate in many systems. A large body of literature exists demonstrating that the provision of supplementary resources can increase the abundance, fecundity and longevity of parasitoids, which in turn should lead to higher parasitism rates (see reviews by Barbosa 1998; Pickett & Bugg 1998; Landis *et al.* 2000). Habitats in which sources of sugar are abundant are particularly likely to be good for parasitic wasps (Shaw 2006) and it has been demonstrated that parasitism decreases as distance from such habitats increases (Baggen & Gurr 1998). Native eucalypt forest and water features within, and adjoining, the study sites were chosen to test this hypothesis as they were thought to provide the best source of supplementary resources in the form of native plants and weedy vegetation. Our results were inconclusive, with only a few weak correlations between distance from landscape features and

parasitism rate. Research into the spatial scale(s) at which *P.atomaria* and *Neopolycystus* sp. locate suitable habitat and hosts would be beneficial in elucidating the influence of landscape features on beetle damage and egg parasitism.

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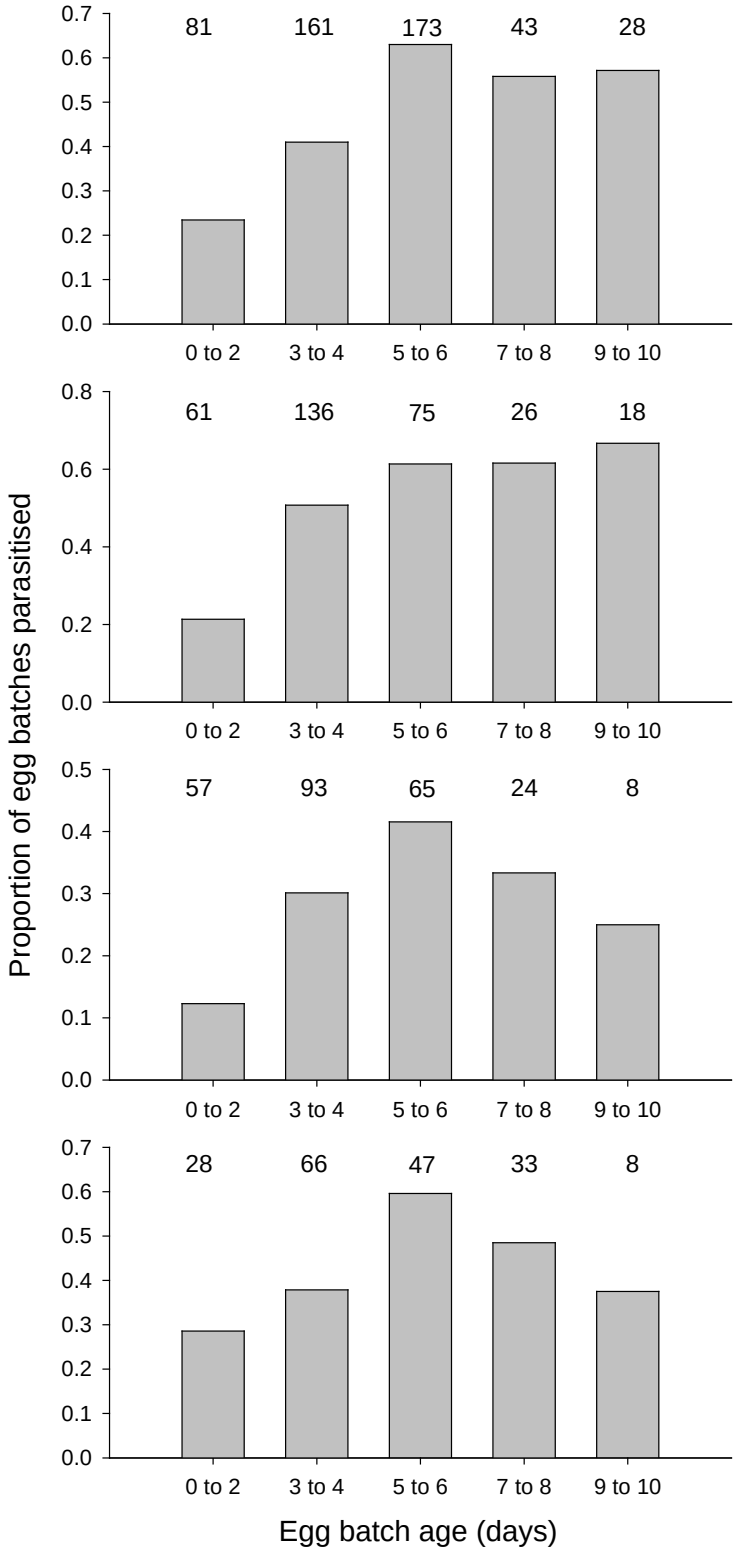
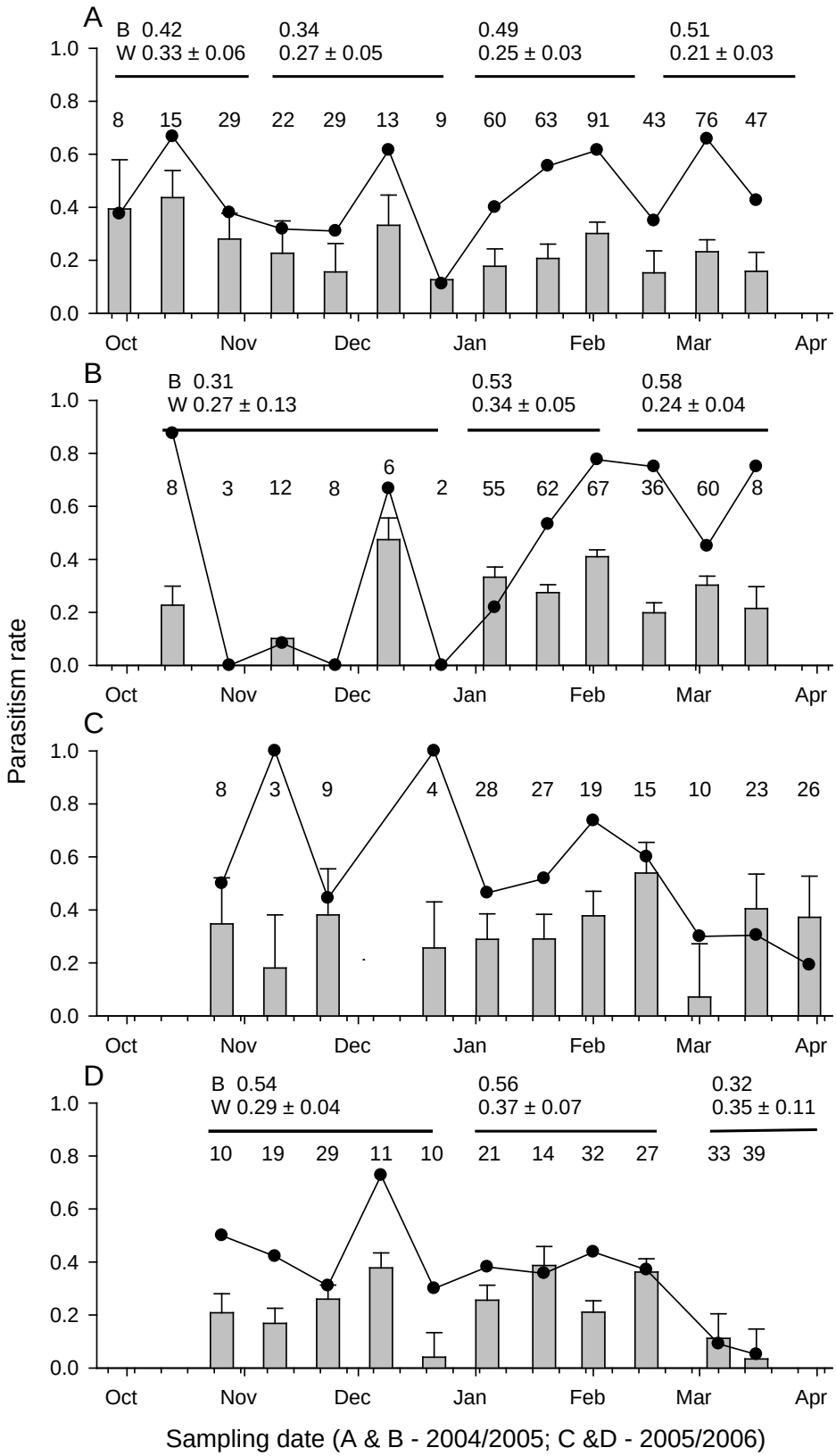
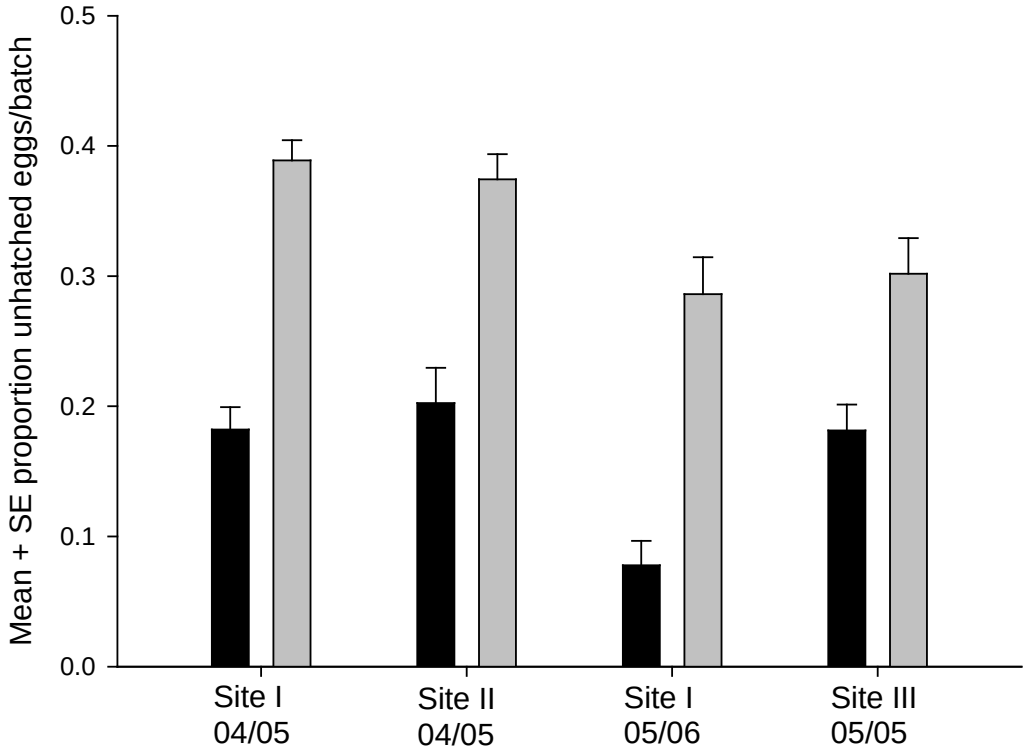

Proportion of egg batches parasitised
81
161
173
43
28
61
136
75
26
18
57
93
65
24
8
28
66
47
33
8
0 to 2
3 to 4
5 to 6
7 to 8
9 to 10
Egg batch age (days)


A
B 0.42
W 0.33 ± 0.06
0.34
0.27 ± 0.05
0.49
0.25 ± 0.03
0.51
0.21 ± 0.03
8 15 29 22 29 13 9 60 63 91 43 76 47
B
B 0.31
W 0.27 ± 0.13
0.53
0.34 ± 0.05
0.58
0.24 ± 0.04
8 3 12 8 6 2 55 62 67 36 60 8
C
8 3 9 4 28 27 19 15 10 23 26
D
B 0.54
W 0.29 ± 0.04
0.56
0.37 ± 0.07
0.32
0.35 ± 0.11
10 19 29 11 10 21 14 32 27 33 39
1.0
0.8
0.6
0.4
0.2
0.0
Oct
Nov
Dec
Jan
Feb
Mar
Apr
Parasitism rate
Sampling date (A & B - 2004/2005; C &D - 2005/2006)


Mean + SE proportion unhatched eggs/batch
0.5
0.4
0.3
0.2
0.1
0.0
Site I
04/05
Site II
04/05
Site I
05/06
Site III
05/05

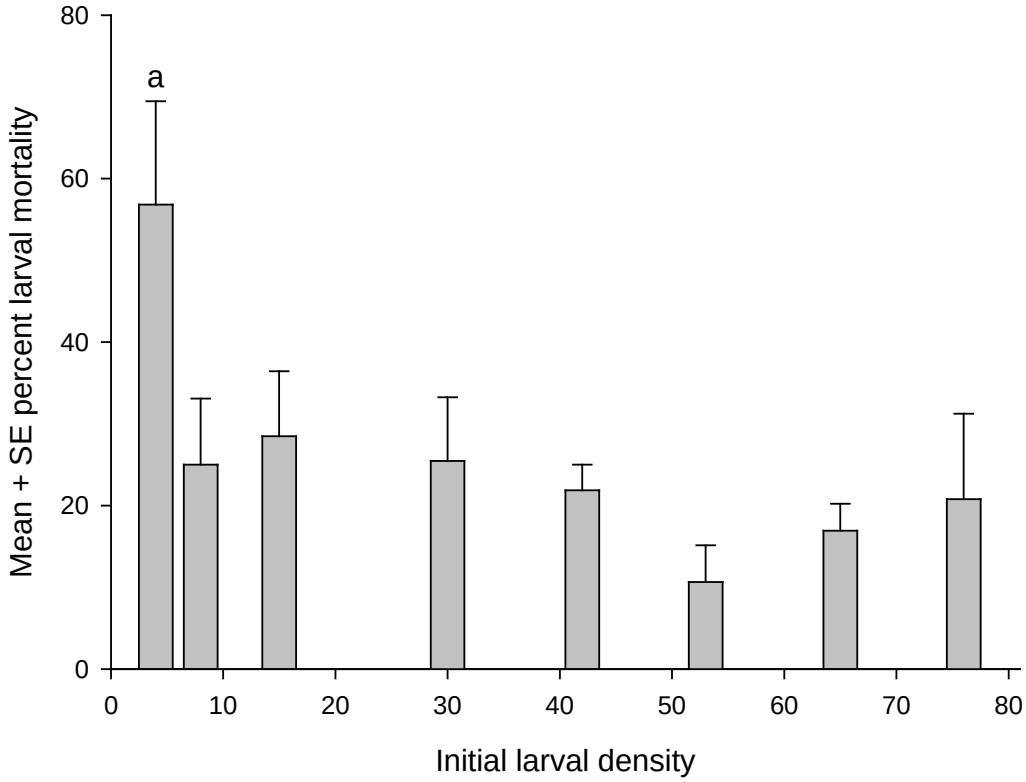

Mean + SE percent larval mortality
Initial larval density
a
0
20
40
60
80
0
10
20
30
40
50
60
70
80

Table 1: Overall proportion of egg batches parasitised, mean ± se number of eggs parasitised within batches, and overall effective parasitism rates by *Neopolycystus sp.* attacking *Paropsis atomaria* at three eucalypt plantation sites in south-east Queensland in 2004/2005 and 2005/2006. Overlaid boxes indicate results of pairwise comparisons between those sites/seasons for between- and within-batch and total parasitism rates. The final row presents results of within-batch variation analyses throughout each sample period (see Figure 3).

	Site II 04/05	**Site I 04/05**	**Site I 05/06**	**Site III 05/06**
Overall between-batch parasitism rate (range across season)	0.52 (0 – 0.87)	0.49 (0.1 – 0.67)	0.47 (0.2 – 1)	0.31 (0.05 – 0.73)
	χ^2_1=0.45, P=0.50	χ^2_1=0.3, P=0.58	χ^2_1=16.7, P<0.001*	
Mean ± se within-batch parasitism rate (range)	0.31 ± 0.02 (0.01 – 0.97)	0.24 ± 0.02 (0.01 – 0.87)	0.30 ± 0.03 (0.01 – 1)	0.22 ± 0.02 (0.01 – 0.74)
	t_{415}=3.4, P=0.001*	t_{309}=1.9, P=0.05	t_{151}=2.0, P=0.04	
Overall effective parasitism rate (range across season)	0.18 (0 – 0.32)	0.13 (0.02 – 0.27)	0.13 (0.02 – 0.27)	0.07 (0.001 – 0.31)
	χ^2_1=91.7, P<0.001*	χ^2_1=5.5, P=0.02	χ^2_1=478, P<0.001*	
Mean ± se between-batch parasitism rate per host generation (range)	0.47 ± 0.1 (0.31 – 0.58)	0.44 ± 0.04 (0.34 – 0.51)	N.D.	0.47 ± 0.09 (0.32 – 0.56)
	t_5=0.33, P=0.75			
Mean ± se within-batch parasitism rate per host generation (range)	0.28 ± 0.04 (0.23 – 0.34)	0.27 ± 0.03 (0.21 – 0.33)	N.D.	0.34 ± 0.03 (0.29 – 0.37)
	t_5=0.38, P=0.72			
Across-season within-batch parasitism rates (Figure 3)	Kruskall-Wallis, H_7=22.1, P = 0.002*	ANOVA, $F_{11,236}$=3.23, P < 0.001*	ANOVA, $F_{10,69}$=1.12, P = 0.36	ANOVA, $F_{9,63}$=2.0 P = 0.047

N.D. number of generations not determined (see Duffy 2007)

*means differed significantly following Bonferroni adjustment for multiple comparisons within data sets (corrected P-value = 0.004)

Table 2: The proportion of egg batches parasitised and within batch parasitism rates of *Paropsis atomaria*, eggs from three eucalypt plantation sites in south-east Queensland in 2004/2005 and 2005/2006 correlated against distance from the nearest native eucalypt forest and nearest source of water. (* designates significant correlation at 0.05 level).

	Site I 04/05	*Site II 04/05*	*Site I 05/06*	*Site III 05/06*
Distance from forest and proportion of egg batches parasitised	r = -0.001 P = 0.993	r = -0.157 P = 0.316	r = -0.039 P = 0.776	r = -0.034 P = 0.773
Distance from forest and within batch parasitism rate	r = 0.069 P = 0.649	r = 0.114 P = 0.542	r = 0.261 P = 0.083	r = -0.320 P = 0.034 *
Distance from water and proportion of eggs parasitised	r = 0.277 P = 0.045 *	r = -0.113 P = 0.471	r = 0.139 P = 0.307	r = 0.144 P = 0.216
Distance from water and within batch parasitism rate	r = 0.033 P = 0.826	r = 0.088 P = 0.638	r = -0.001 P = 0.995	r = 0.136 P = 0.380

Figure 1: Proportion of *Paropsis atomaria* egg batches parasitised after exposure to wasps in the field for different time periods at three eucalypt plantation sites in south-east Queensland in 2004/2005 and 2005/2006 [Site I 04/05(A), Site II 04/05 (B), Site III 05/06 (C), and Site I 05/06 (D)]. Numbers above bars represent the number of egg batches in each age class.

Figure 2: Between (lines) and mean + se within (bars) batch parasitism rate of *Paropsis atomaria* egg batches by *Neopolycystus* sp. at three eucalypt plantation sites in south-east Queensland in 2004/2005 and 2005/2006. Horizontal lines approximate the duration of host generations, and between- (B) and within- (W) egg batch parasitism rates for each. Numbers associated with each data point represent the number of egg batches collected [Site I 04/05 (A), Site II 04/05 (B), Site I 05/06 (C), and Site III 05/06 (D)].

Figure 3: Mean + se proportion of *Paropsis atomaria* eggs per batch that produced neither wasps nor larvae from batches which were unparasitised (white) and parasitised (grey) from three eucalypt plantation sites in south-east Queensland in 2004/2005 and 2005/2006.

Figure 4: Mean + se percentage *Paropsis atomaria* first instar larval mortality at different initial densities on new season's expanded *Eucalyptus cloeziana* foliage after one week. 'a' designates the mean that differed significantly from all others (Fisher's LSD post-hoc test).